

## **Diapause Duration as a Synchronizer of Parasite (*Peristenus* spp: Hymenoptera: Braconidae) and Host (Hemiptera: Miridae) Life Cycles, and its Use in Separating Morphologically-similar Parasite Species**

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### **ABSTRACT**

Five nominal species of braconid wasps that parasitize nymphs of five mirid species were studied on farms. The biological data obtained indicate that *Peristenus pallipes* (Curtis) is likely two (and possibly three) distinct species. In alfalfa and alfalfa-forage grass fields, there were clear parasite:mirid host associations: *P. pallipes* "A": *Leptopterna* and *Trigonotylus*; *P. pallipes* "B": *Adelphocoris*; *P. pallipes* "C": *Lygus*; *P. digoneutis*: *Lygus*; *P. conradi*: *Adelphocoris*; *P. pseudopallipes*: *Lygus*; and *P. howardi*: *Lygus*. Diapausing adults of these parasite species do not emerge from their cocoons immediately after the cocoons are removed from cold storage; this delay is referred to here as diapause "duration". Average diapause duration varied from 8 to 61 days, depending on the parasite species, and each duration was statistically different from that of the other species. These durations corresponded to the temporal sequence of appearances of nymphs of the appropriate mirid host species during the growing season, and serve to synchronize the emergence of parasite adults with the hatching of their preferred hosts. All parasites studied except *P. digoneutis* and *P. howardi* are univoltine. The latter two species produce some non-diapausing progeny in their first generation, which emerge promptly, enabling these species to parasitize second generation mirids. The unusually prolonged emergence period of *P. howardi* suggests that the second generation of this species may be partly produced by late-emerging (long-duration) parasites from the previous year, or perhaps by a very similar (sibling) species. Diapause rapidly increased in both *P. digoneutis* and *P. howardi* collected in hosts within two weeks after the maximum photoperiod occurred (June 21) in the field.

**KEY WORDS** *Adelphocoris*, alfalfa, biological control, diapause, *Leptopterna*, *Lygus*, parasites, *Peristenus*

Diapause in parasites of mirid nymphs has two essential functions. It is a temperature-independent timing system that prevents the fully-formed adult parasites from emerging from their cocoons during temporary warm periods in the fall or winter, when there are no hosts. Later when warm weather arrives, diapause further delays the emergence of the short-lived adult wasps so each parasite species will emerge from their cocoons at the same time that nymphs of the appropriate mirid species are present. Data on the latter function, the delayed emergence of both univoltine and bivoltine parasites to coincide with the hatching of mirid nymphs, referred to here as diapause "duration", will be presented in this paper, along with additional information on the often large differences in diapause duration between related *Peristenus* species.

A total of four native and introduced species of *Peristenus* parasitize nymphs of four of the seven mirid species that feed on alfalfa and alfalfa-grass hay crops

sample could not be processed immediately, it was stored at Newark at 13° C to minimize mortality. All samples were processed within one day of collection.

### Laboratory rearing

Rearing was done to obtain the adult stage needed for identification of the various parasite species (Day 1994). All field counts and mirid species identifications were verified (and corrected if necessary) before one or more subsamples of each mirid species (maximum 40 nymphs each) was placed in a ventilated plastic cage (details in Day 1996). All rearing was done in an environmental chamber at  $22 \pm 2^\circ\text{C}$ ,  $65 \pm 10\%$  RH, and a photoperiod of 16:8 (L: D) h. Each cage was fed "bouquets" of greenhouse-grown alfalfa or grass seed heads, depending on the mirid species, every 3-5 d as needed for the next 3 wk. By this time, all primary parasite larvae had matured, killed their mirid hosts, dropped through the screened false bottom of their cage, and pupated in the artificial soil (damp vermiculite) on the cage bottom. A filter paper disk under the vermiculite prevented parasite cocoons from adhering to the plastic cage bottom, and also facilitated the transfer of the vermiculite to a smaller ventilated emergence cup twice—at 11 d and 22 d. This procedure is necessary because non-diapausing parasites may emerge as early as 13 days, and could parasitize surviving mirid nymphs, biasing the proportion that were parasitized data. Each of these two cups per cage were checked 3-5 times per wk for emergence of non-diapausing primary and secondary parasites, for 3 wk. After this period the emergence cups were moved to an outdoor insectary, where they remained until December 1-5.

### Overwinter storage and Spring emergence

All rearing cups were moved from the insectary on December 1-5 to a refrigerated room ( $2 \pm 1^\circ\text{C}$ ). The combination of summer and fall outdoor temperatures, plus cold winter storage, terminated diapause by 1 March for all parasite species except about 20% of *P. howardi* (research on diapause of this species is continuing). On March 1-5, all sample cups were returned to the same environmental chamber ( $22^\circ\text{C}$ , 65% RH, 16L: 8D PP) for emergence of the adult parasites. The number of days required for emergence of each adult, of each parasite species, was recorded. All parasites were identified to species by the author. Voucher specimens of all species are in the reference collection of the Beneficial Insects Research Laboratory, and in the Canadian National Collection in Ottawa, where Dr. Henri Goulet (Agriculture Canada) is presently working on a revision of the genus.

### Calculation of percentage parasitized

An aliquot of each sample of mirid nymphs collected was stored at  $-15^\circ\text{C}$ , in a non-frost-free freezer, for later dissection. This provides much more accurate estimates of the percentage of nymphs that were parasitized than does rearing, because more parasitized nymphs (and the parasites inside) die before maturing than unparasitized nymphs (Day 1994).

### Post-emergence dissection of unemerged parasite cocoons.

After all parasite emergence had been completed, all unemerged cocoons were saved for later examination. Aliquots were dissected to determine if any still contained living adult parasites, which remained in diapause.

## RESULTS AND DISCUSSION

### Basic information

Table 1 lists the insects that will be discussed in this paper—five nominal species of parasites in the genus *Peristenus*, the five species of mirids that they attack, the “preferred” (best adapted) hosts of each parasite species as demonstrated by parasitism rates in nature (Day 1999, Day et al. 1999), and the host plants of the mirids in alfalfa and alfalfa-grass hayfields.

### Diapause “duration”

Table 2 shows that diapause “duration” (the average time required for an adult to emerge from its cocoon, after the cocoon has been moved from cold storage to room temperature) varies considerably among the parasite species, from as little as eight days to as long as 61 days. The shortest duration species attacks the earliest-appearing mirids, and the longest duration species attacks the latest-appearing mirids, as will be further discussed below. The considerable difference in diapause duration between *Peristenus* “*pallipes* A” (8 days), which parasitizes grass-feeding mirids, and *Peristenus* “*pallipes* B & C” (19 days), which parasitizes legume-feeding mirids, suggests that *P. “pallipes”* is at least two distinct species. Although there were no diapause duration differences between “*P. pallipes* B & C”, taxonomic studies now underway suggest that these may be separate species.

### Multi-voltine species.

Note (Table 2) that two parasites (*P. digoneutis* and *P. howardi*) produce some non-diapausing progeny in each generation. These do not undergo any delay (diapause) in development; adult parasites emerge within a few weeks, and parasitize second generation mirids in the same year, greatly increasing their usefulness in biological control.

### Variability of diapause length.

Diapause duration for all but one of the six *Peristenus* species groups in Table 2 had a range of only 6-11 days, showing the precision of the timing mechanism of these tiny (2-3mm) parasitic wasps. The reason for the much longer range (50 days) in *P. howardi* is not known—perhaps the scarcity of summer rainfall where this species is found (Idaho, eastern Washington) causes a greater variability in the date its mirid host nymphs appear from year to year (making synchronization difficult), or perhaps *P. “howardi”* is actually a complex of two (short and long duration) species. In either case, the data suggest that second-generation *P. howardi* are partially produced by long-duration (late emerging) parasites from the previous year, and not only by non-diapausing first generation adults.

### Use of life cycles to separate species.

When research on the parasites of mirid pests was in its early stages in the 1960's, the univoltine *P. “pallipes”* was reared from mirid nymphs collected over a very long period (May to August, Loan 1965). Subsequently, Loan (1970) concluded that these morphologically-similar wasps were actually two species,

*P. pallipes* (May-June) and *P. pseudopallipes* (July-August). The three distinct levels of diapause duration observed in the present study (Table 2: 8 vs. 19 vs. 45 d) confirm Loan's conclusion, and further indicate that what is presently known as *P. pallipes* is likely to be at least two (A vs. B/C) additional species, as Loan and Shaw (1987) suspected.

#### **Life cycle of *P. digoneutis***

This is the only species discussed here that consistently produces two generations (and often a partial third) each year. Table 3 shows that only 39% of its first (June) generation diapauses, so most parasites emerge promptly, and attack second generation tarnished plant bugs. This increases the biocontrol effectiveness of *P. digoneutis*, because it parasitizes both of the two principal generations of the target pest in the northeastern U.S. (Day 1996). Nearly all of the second generation of *P. digoneutis* diapause (Table 3), which is appropriate as the third host generation is small. Diapausing first and second generation *P. digoneutis* emerged at about the same time (average 15 and 17 days respectively,  $n=34, 59$ ) the following year. This indicates that they both produce first generation parasites, and therefore that second generation parasites can only be produced by non-diapausing first generation parasites.

#### **Lengthening diapause duration**

Doubling the cold period (Fig. 1) slightly reduced diapause duration for both of the bivoltine parasites. Similar results for European *Peristenus* spp. (Pawinska and Varis 1990) and an ichneumonid parasite (Slovak 1988) have been reported, and are evidence of an internal "clock" that modifies its responses to changing external stimuli (Saunders 1976), to better synchronize developmental times.

#### **Photoperiod**

Because daylength on the same date does not change from year to year, it is likely that photoperiod is the principal regulator of diapause in the two species of *Peristenus* that do not have an obligatory diapause. There is a sudden increase in diapause for both *P. howardi* and *P. digoneutis* (Fig. 2) that were collected soon after the maximum photoperiod on June 21. Diapause was likely programmed in the parasite very early, by the female parent before the egg is laid (Brodeur and McNeal 1989), or in the parasite egg or small larva within the mirid host (Brown and Phillips 1990), because all parasites were reared (in their nymphal hosts) under a long-day photoperiod (16L:8D) in the laboratory, within 1 day of their collection, but diapause still occurred in the later samples.

#### **Parasite-host synchronization**

The diapause duration data (Table 2) have been superimposed on mirid field population data in Figure 3, to illustrate the temporal sequences of the various mirid species and generations, and the corresponding emergence times of the parasites that attack them, at the two locations. This figure demonstrates that diapause duration can synchronize parasite emergence with the appropriate host, and that all of the parasite species native to the northeastern U.S. (*P. pallipes* A, *P. pallipes* B & C, and *P. pseudopallipes*) are sequenced correctly. One of the introduced parasites (*P. digoneutis*) is synchronized with its principal host (*L. lineolaris*), while the other (*P. conradi*) appears to be slightly late for its host, but genetic

selection may correct this over time. As mentioned earlier, all diapausing *P. digoneutis* emerge at the same time (1<sup>st</sup> generation hosts), so second generation mirids are parasitized only by non-diapausing parasites, which are not shown in this figure.

### *P. howardi*

This northwestern parasite appears (Fig. 3) to emerge between its target host's (*L. lineolaris*, in the northeastern U.S.) generations I and II. However, its emergence period is so prolonged (Table 2, 50 days) that this would allow it to attack both mirid generations. Because it has not become established at Newark (only modest numbers have been released to date: Day, unpubl.), its actual synchronization in northeastern alfalfa fields cannot yet be determined.

Each year, many diapausing *P. howardi* fail to emerge. For example, in 1999 (the year after they were collected) dissections of a subsample of unemerged cocoons indicated that many were still alive, but remained in diapause. After they were subjected to a second winter regimen, about 10% of these broke diapause, and emerged in 2000 — two years after they had been collected in their hosts. Later dissections showed that all remaining cocoon contents were dead. It is not known if this delayed emergence is a natural survival mechanism, or if it is an artifact of our laboratory conditions.

### Insights on the origin of parasites

If *P. pallipes* "A" (reared from *Leptopterna* and *Trigonotylus*) and/or *P. pallipes* "B" (reared from *Adelphocoris*) are eventually described as new species distinct from *P. pallipes* "C" (reared from a native *Lygus*), the origins of "A" and "B" will need to be explained. All three of their mirid hosts are accidentally-introduced pests (Table 2), but *P. pallipes* A and B are not known from any native mirid species (Day 1999).

### Usefulness of diapause duration.

This biological characteristic provides the means for each parasite species to synchronize the emergence of its adults with the hatch of nymphs of its preferred host species. The considerable differences in duration noted in this paper provide entomologists with an additional, new method for separating morphologically similar parasite species.

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### DEDICATION

This paper is dedicated in memory of Conrad C. Loan, a Canadian entomologist (1926-1999) who "brought order out of chaos" by his series of clarifications of the taxonomy of *Peristenus*, *Leiophron*, and *Microctonus* species during the 1960-1987 period. Our laboratory could not have developed successful on-

farm biological control systems for the tarnished plant bug and alfalfa weevil without the greatly-improved species identifications that Conrad developed. Fortunately, this work is currently being extended by Henri Goulet, also at Ottawa.

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Table 1. The *Peristenus* species that parasitize mirid pests of alfalfa-grass crops, and their host preferences as demonstrated by parasitism levels.

<i>Peristenus</i> species	Mirid host	Host Plant <sup>a</sup>	Average peak parasitism <sup>b</sup>
<i>P. pallipes</i> (Curtis) A	<b><i>Trigonotylus caelestialium</i></b> (Kirkaldy) (small green grass bug)	G	<b>43%</b>
A	<b><i>Leptopterna dolabrata</i></b> (L.) (meadow plant bug)	G	<b>37%</b>
B	<b><i>Adelphocoris lineolatus</i></b> (Goeze) (alfalfa plant bug)	A	6%
C	<i>Lygus lineolaris</i> (Palisot) (tarnished plant bug)	A	5%
<i>P. conradi</i> Marsh	<i>Adelphocoris lineolatus</i> (Goeze)	A	<b>22%</b>
	<i>Lygus lineolaris</i> (Palisot)	A	7%
<i>P. digoneutis</i> Loan	<i>Lygus lineolaris</i> (Palisot)	A	<b>31%</b>
	<b><i>Adelphocoris lineolatus</i></b> (Goeze)	A	6%
<i>P. howardi</i> Shaw	<i>Lygus hesperus</i> Knight (western tarnished plant bug)	A	<b>65%</b>
<i>P. pseudopallipes</i> (Loan)	<i>Lygus lineolaris</i> (Palisot)	A	9% <sup>c</sup>

Mirid common names in parentheses are from the ESA official list. Species in **bold** type are not native to North America: 3 mirids were accidentally introduced via commerce, and 2 parasites were introduced for biological control. *P. pallipes* may actually be 3 species, denoted here as A, B, & C. Data for all species are from New Jersey or Delaware (except *P. howardi*, from Idaho). Additional details are in Table 2 and text.

<sup>a</sup>G = grasses (timothy, orchard grass), A = alfalfa.

<sup>b</sup>Data are averages of peak parasitism per year, 1988-1995, and are from Day 1999, except *P. howardi* data are from Day 1997-1998 (unpubl.). Parasitism rates on preferred hosts are in **bold** type. Parasitism by *P. digoneutis* was much higher before it reduced its host (Day 1996).

<sup>c</sup>Parasitism is much higher on *Erigeron* (*Conyza*), a native weed (Compositae/Asteraceae) (Shahjahan & Streams 1973, Lim and Stewart 1976, Day unpubl.).

Table 2. Differences in emergence sequence (diapause duration) and number of generations between different *Peristenus* species.

Sequence/ Parasite	No.of gener.	Source	Principal Hosts <sup>b</sup>		Sample size	Parasites		
			mirid species	major gener.		Days to emergence		
						range	diff.	average <sup>c</sup>
1. <i>P. pallipes</i> -A	1	NJ	<i>Leptopterna</i> , <i>Trigonotylus</i>	1 2	350	4-14	11	8a
2. <i>P. digoneutis</i>	2+	NJ	<i>Lygus</i>	2	80	8-17	10	14b
3. <i>P. pallipes</i> -B	1	NJ,	<i>Adelphocoris</i>	2	134	16-25	10	19c
<i>P. pallipes</i> -C	1	DE	<i>Lygus</i>	2	47	16-25	10	19c
4. <i>P. conradi</i>	1	DE	<i>Adelphocoris</i>	2	234	22-27	6	25d
5. <i>P. pseudopallipes</i>	1	DE	<i>Lygus</i>	2	62	39-48	10	45e
6. <i>P. howardi</i>	1-2	ID	<i>Lygus</i>	1-2	225	37-86	50	61f

**Bold type** identifies intentionally (parasites) or accidentally (mirids) introduced species.

Data are from 1993-1996 collections for all species but *P. howardi* (1998-2001 collections).

<sup>a</sup> *P. "pallipes"* is suspected to be two or more morphologically-similar species (Loan & Shaw 1987). Three groups (A-B-C) have been separated here, based on diapause duration and mirid host species. Parasites with a "+" generation may have an additional generation, if hosts are abundant.

<sup>b</sup> For additional details, see Day 1999 (all species except *P. howardi*) and Day et al. 1999 (*P. howardi*).

<sup>c</sup> Average number of days at 23°C, after diapausing parasite cocoons were removed from cold storage (1.7°C). Averages were calculated from a random sample of 10 emergence days per species (selected from total sample sizes listed in table), to provide the uniform sample size for each species needed for the statistical analysis. The lower-case letters indicated that all means are significantly different [ANOVA: df 45, F=96, P>0.01; and Duncan's MRT:  $s_x = 2.07$ , P>0.05; (Steele & Torrie 1980)]. Days to emergence may vary somewhat between locations and years (Day unpubl.) probably due to climate differences and weather variations, respectively, but the sequence of species appearance remains the same.



Table 3. Differences in diapause incidence between generations of *P. digoneutis* parasitizing *Lygus* in the field. Blairstown, NJ 1993-2001.

Year	Generation I			Generation II		
	total	diapausing		total	diapausing	
1993	16	3	(19%)	12	11	(92%)
1994	2	0	(0%)	15	13	(87%)
1995	26	21	(81%)	26	8	(31%)
1996	4	4	(100%)	26	26	(100%)
1997	18	6	(33%)	77	77	(100%)
1998	36	13	(36%)	10	10	(100%)
1999	6	0	(0%)	2	1	(50%)
2000	5	0	(0%)	10	7	(70%)
2001	14	0	(0%)	1	0	(0%)
Totals	127 <sup>a</sup>	47		179 <sup>a</sup>	153	
Weighted average		(37%) <sup>b</sup>			(85%) <sup>b,c</sup>	

<sup>a</sup> Sample sizes decreased as parasitism by *P. digoneutis* reduced *Lygus* numbers (Day 1996).

<sup>b</sup> The proportions of parasites diapausing in the two generations are significantly different at  $P > 0.005$  ( $\chi^2 = 77.1$ , df 1; Steele & Torrie 1980). In most years, Gen. I occurs in June and Gen. II in July, at this location.

<sup>c</sup> In most (67%) years, not all second generation *P. digoneutis* diapaused. This indicates that a small third generation would be produced in the field if host nymphs are present. Small numbers of third generation parasites were detected in August and early September samples, in 4 of these 9 years.

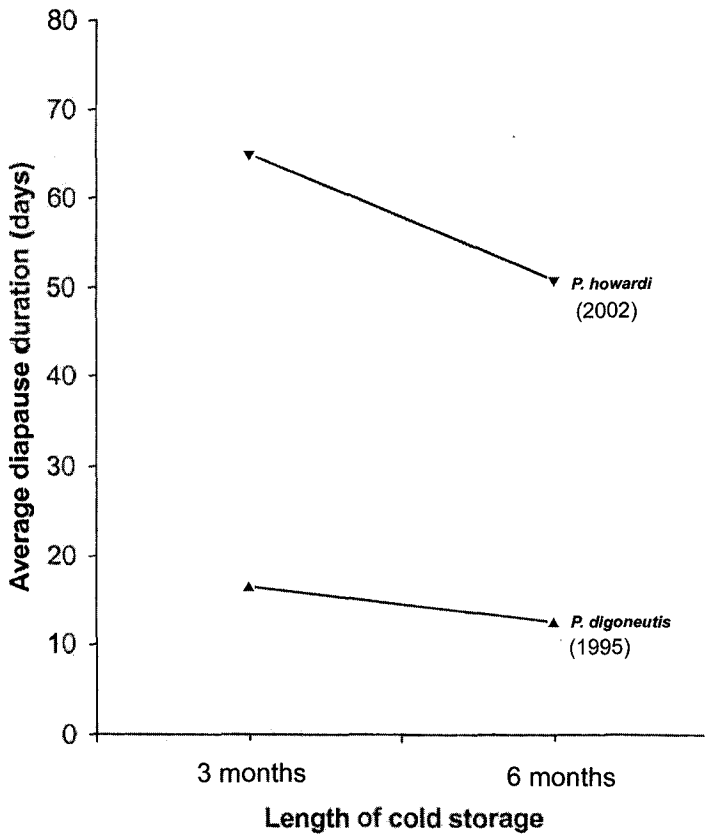


FIG. 1. Duration of diapause of two species of bivoltine *Peristenus* after short and long cold storage periods. Both 6-month diapause durations were significantly shorter than the 3-month durations [ANOV: df 7,1; F12.8,  $P > 0.01$  (*P. howardi*); df 7,1; F14.9,  $P > 0.01$  (*P. digoneutis*)].

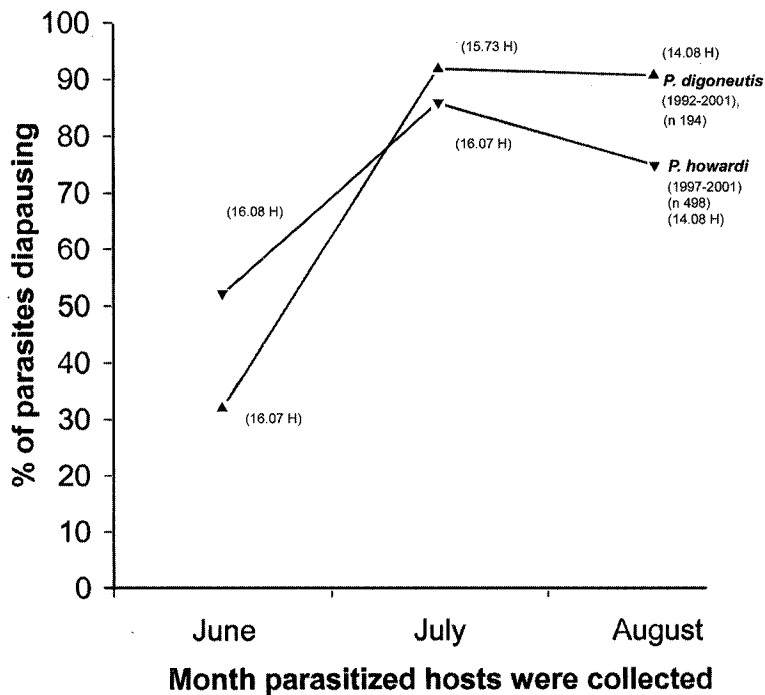


FIG. 2. Influence of collection date on diapause incidence in two bivoltine species of *Peristenus*, at two locations. Daylengths on the 21<sup>st</sup> of each month, the number of parasites of each species included in the analyses, and the years these data were collected, are in parentheses. *P. digoneutis* rates differed between June and July (df 2,  $\chi^2 = 116$ ,  $P > 0.001$ ), and *P. howardi* rates differed between June and July (df 1,  $\chi^2 = 27$ ,  $P > 0.001$ ), and between July and August (df 1,  $\chi^2 = 3.95$ ,  $P > 0.05$ ).

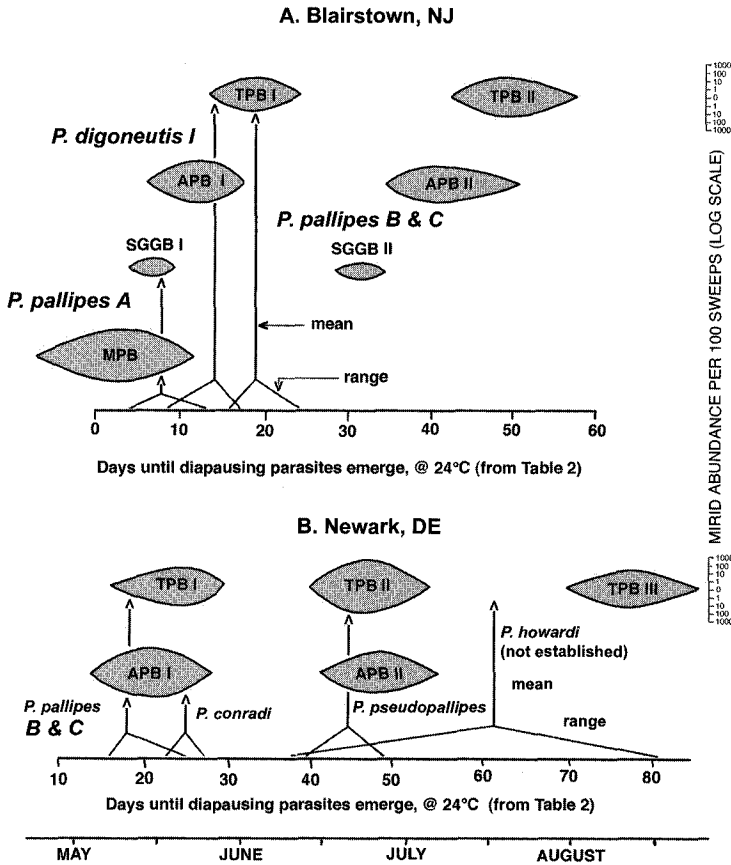


FIG. 3. Diagram of the dates that mirid nymphs occur in the field (bottom scale), the relative sizes of each population (log scale), and the synchronization of emerging overwintering parasites as regulated by diapause duration, at two locations. Data are averages of 1993-1996 data for all species except *P. howardi* (1998-2001 data). To save space, mirid common names (Table 1) are abbreviated as follows: APB (*Adelphocoris*), MPB (*Leptopterna*), TPB (*Lygus*), and SGGB (*Trigonotylus*). Roman numerals denote mirid generations.